

Energy Flow and Trophic Relations in Soil Communities: State of Knowledge Two Decades after the International Biological Programme

by

HENNING PETERSEN*

Based on the review of Petersen and Luxton [1982] and subsequent publications on soil fauna productivity the present knowledge about energy flow through soil communities is surveyed in order to demonstrate some approaches which seem promising for future research. An evaluation of the available information concludes that practically all data sets for metabolism and productivity of soil fauna communities have been derived indirectly from field density and biomass data, combined with laboratory measurements of metabolic parameters. Community respiration of the total fauna in 26 different natural, semi-natural or agricultural soils was correlated closely with biomass indicating a mean respiration rate of 0.1 KJ per mg dry weight biomass. Positive correlation between NPP and total soil faunal respiration is found only when high arctic sites are compared with sites in milder climatic regions. Total soil faunal respiration and amounts of litter input were not correlated in the data examined. The problem of coping with the complexity of the soil biota in energy flow studies is discussed and illustrated by examples of computer models which attempt to compromise between simplification and preservation of the large taxonomic and functional diversity of the soil community. The effect on productivity and energy recirculation of changing the energetic efficiency ratios used in an energy flow model is illustrated.

Introduction

The International Biological Programme (IBP), 1964–1974, was a world-wide, multidisciplinary research effort with the objective to examine “the biological basis of productivity and human welfare” [IBP News 1, 1964. International Council of Scientific Unions]. Productivity of terrestrial ecosystems was one of the main themes of the programme, and several studies of the structure and pro-

*Natural History Museum, Mols Laboratory, Strandkaervej 6–8, Femmøller, DK 8400 Ebeltoft, Denmark.

duction ecology of terrestrial ecosystems were implemented in a wide range of climatic regions and plant communities. Main emphasis was laid on natural or semi-natural ecosystems whereas the subsequent Man and Biosphere programme [UNESCO 1971] focused on the impact of man on ecosystems.

Only a minor part of the ecosystem research projects within the IBP included ecological studies of the biotic communities in the soil. Nevertheless, these studies considerably extended the data base for conclusions about the ecology of soil organisms and, in particular, the energy flow and nutrient circulation through soil communities. The effort by the IBP projects in these fields was inspired greatly by the pioneer work of Bornebusch [1930] and later works such as those of Macfadyen [1963] and Kitazawa [1971].

The information available at the end of the IBP-period on density, biomass, resource utilization and production ecology of fungal- and animal communities in soil and litter, was reviewed and synthesized by Kjøller and Struwe [1982] and Petersen and Luxton [1982].

At the time when these works were completed many results from the IBP-projects were still unpublished. Some ecosystem projects were continued beyond the official end of the IBP and others were initiated outside the framework of IBP [e.g. Persson et al. 1980, Schaefer 1990]. A few multidisciplinary research projects initiated during the late seventies and eighties have investigated the production ecology of agro-ecosystems under different management regimes [Hendrix et al. 1986, Andrén et al. 1990]. Detailed studies of population dynamics, resource utilization etc. of single species or soil faunal communities have added to our understanding of the functioning of the soil community [e.g. Takeda 1984, 1987, van Straalen 1985, 1989]. The indirect role of the soil fauna as regulators of energy and nutrient transfers in the litter and soil has been elucidated by the works of J.M. Anderson and his school at the University of Exeter, U.K. [e.g. Hanlon and Anderson 1979, Anderson and Ineson 1983], Seastedt [1984] and others. Finally, a renewed interest in productivity studies has emerged recently in connection with the concern for the effect on ecosystems of toxic chemicals and other anthropogenic disturbances [van Straalen 1989].

For the reasons mentioned above, it may be worthwhile looking at the energy flow issue once more with a view to updating the information presented in Petersen and Luxton [1982]. However, instead of the comprehensive review and detailed comparison of data aimed at in that paper, emphasis will be laid here on the search for possible general relationships and on the demonstration of a few types of approaches with a view to understanding the way energy is channelled through the litter and soil compartments of the ecosystems. Although the title of this paper implies the treatment of the whole soil community including the microflora this presentation will focus on the soil fauna community and consider the microflora only as a food source for the soil fauna, i.e. as the basic level of the

decomposer food web.

Energy Flow and Food Webs

The energy flow may in simplest terms be represented by the equations:

$$C = F + R + P$$

and

$$A = R + P$$

where: C = consumption, F = defecation (including excretion), R = respiration, P = secondary production (growth and reproduction), and A = assimilation.

The production at one trophic level constitutes the resource for the next higher trophic level. In this way the energy flows between biotic components at different trophic levels make up the food web of the biotic community. The term "energy flow" is perceived by some authors as synonymous with assimilation, but energy is also transferred in faeces and excreta and in that way recirculated within the system. Therefore, it is preferred to define energy flow here as the complex of individual energy transfers passing through the food web, including those which return energy to the base of the trophic system [figure 6].

Evaluation of the Energy Flow Data

Petersen and Luxton [1982] attempted to provide a basis for evaluation of the density and biomass data for soil fauna communities available in the literature. It was argued that size, number, depth and localization of sample units, sampling period and frequency as well as sampling and extraction methods were crucial factors determining the reliability of the density estimates. Biomass estimates have, in most cases, been calculated by multiplication of density estimates by average weight per specimen. Therefore, the reliability of the biomass estimates depends both on the density estimates and on the estimates of average individual weight. The last mentioned estimate may easily be biased if it is not representative for the whole size distribution within the populations through the whole investigation period.

In nearly all studies of energy flow through the soil faunal community, estimates of population metabolism in the field have been derived indirectly by computations based on density and biomass estimates, combined with laboratory data for isolated specimens under controlled conditions. Mostly, the equations for calculating the metabolic quantities have been borrowed from the literature and applied to more-or-less narrow subgroups within the decomposer community considering the general relationship between individual weight and metabolic rate. Thus, a common procedure seems to be the following: Population respiration for composite taxonomic groups is calculated from field density, biomass

and temperature data by using regression equations which relate respiration to weight and temperature. Secondary production and assimilation are calculated subsequently from the estimate of population respiration by means of regression equations which relate production with respiration [McNeill and Lawton 1970, Humphreys 1979], or by means of ratios between production, respiration and assimilation [Heal and McLean 1975, Petersen and Luxton 1982]. Finally, consumption and defecation rates are calculated from the assimilation estimate using estimates for assimilation efficiency [e.g. Heal and MacLean 1975, Petersen and Luxton 1982].

Alternatively, consumption estimates for field populations have been based on laboratory measurements of average consumption rates as a percentage of body weight combined with data on weight distribution within the field population [e.g. Luxton 1981].

In any case, it should be realized that practically all available data on energy flow quantities at the population or community level are in reality more or less sophisticated transformations of density and biomass data adjusted to account for field temperatures.

Exceptionally, it has been possible to estimate production of field populations of soil animals directly by analysis of the size or age structure of the population based on repeated field samplings through the year. The requirement, rarely met in soil fauna populations, is the ability to distinguish even-aged cohorts of specimens which can be followed through the development time and used for calculation of survivorship curves.

This approach employed by van Straalen [1989] for two litter dwelling Collembola species, *Orchesella cincta* and *Tomocerus minor*, resulted in much higher estimates of relative productivity (P/B) than previously reported for Collembola, i.e. 8.3 yr⁻¹ and 6.7 yr⁻¹, respectively, as compared with ratios between 1.4 yr⁻¹ and 4.8 yr⁻¹ reviewed by Petersen and Luxton [1982]. However, as pointed out by van Straalen [1989], differences between the metabolic rates of individual collembolan species, which appear to be correlated with their depth distribution [cf. Petersen 1980], may also contribute to the high relative production rate of the two surface-living Collembola. At any rate, the contribution of the Collembola to the energy flow of the total soil community in van Straalen's pine stand at Dronten, the Netherlands, was considerably more significant than previously reported for other ecosystems. Thus, the consumption of the collembolan community was calculated as 600 KJ·m⁻² which is equivalent to about 6% of the annual leaf litter fall.

Estimates of soil microbial productivity have generally been obtained by calculations based on biomass estimates which may again have been calculated from estimates of bacterial counts or hyphal lengths [Kjøller and Struwe 1982]. However, because microfloral respiration generally dominates the total soil meta-

bolism strongly the productivity may also be estimated from the total input of dead organic matter to the soil, provided that a steady state of soil organic matter is assumed. Alternatively, the microbial respiration may be estimated from measurements of total efflux of carbon dioxide from the soil.

Provided the estimate for microbial metabolism has not been based on one of the two last-mentioned methods these can be used as independent checks on estimates of total energy flow through the soil community. Thus, for a conventionally-tilled agricultural soil Hendrix et al. [1987] found surprisingly good agreement between estimates for total heterotrophic respiration calculated on the basis of field biomass estimates and estimates of either carbon input by plant residues or carbon dioxide efflux from the soil. Parallel no-tillage plots in the same field showed less agreement between the three independent methods. For a Swedish pine forest soil, Persson et al. [1980] found that the heterotrophic soil organisms together respired $228 \text{ g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ whereas the annual input to soil was estimated as $264 \text{ g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$. This suggests an accumulation of $47 \text{ g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ corresponding to a 1 % increase of dead organic matter per year. However, as the authors point out, considering the inaccuracy of the estimates it is in reality impossible to conclude whether the accumulation rate is 1 or 2 percent or does not occur at all.

Comparison of Soil Faunal Metabolism in Different Sites

The following comparisons of soil community metabolism have been based on studies where energy flow data are available for practically the whole soil faunal community. Most of the studies used in the comparison were treated in Petersen and Luxton [1982] but final results of the Solling beech forest project in Germany [Ellenberg, Mayer and Schauer mann 1986], results from a German beech forest on limestone [Schaefer 1990] and data from a few energy-flow studies of agro-ecosystems [Golebiowska and Ryszkowski 1977, Hendrix et al. 1987, Andrén et al. 1990] have been added.

The analysis here only treats community metabolism in the sense of community respiration because, as stated above, the other quantities of energy flow have generally been calculated by multiplication of the community respiration data by mostly identical factors borrowed from literature.

Protozoa have been omitted from the comparisons because studies of this group of organisms have been neglected in nearly all available data sets. It has become evident, however, that protozoan metabolism may be more significant than the metabolism of any of the metazoan soil fauna groups. Thus, the Protozoa constituted more than 20% of the total faunal respiration in a Swedish pine forest soil [Persson et al. 1980] and between 37 and 52% of total soil faunal respiration in Swedish agricultural fields [Andrén et al. 1990].

Figure 1 shows the relationship between dry weight biomass and annual respiration of the total soil fauna community for a wide range of ecosystems representing high arctic tundra, alpine moorland, temperate grassland, boreal coniferous woodland, temperate deciduous woodland and temperate agricultural land. Unfortunately, subtropical or tropical ecosystems are only represented by one point in this graph [Lamotte 1989]. To the author's knowledge no other

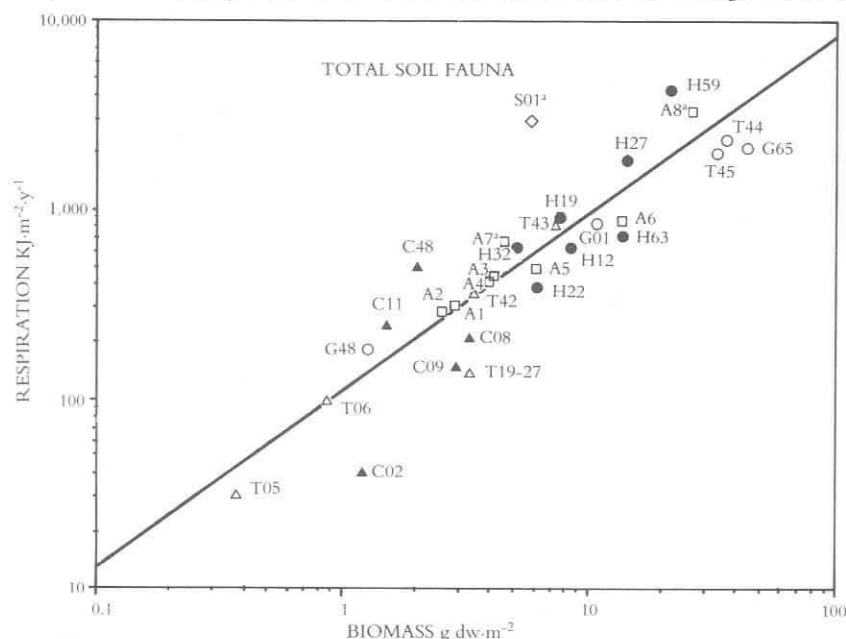


Figure 1. Relationship between community respiration and biomass of the total soil fauna (excl. Protozoa). — Agricultural soils (□), Tundra and montane moorland (△), Temperate grassland (○), Tropical savanna (◇), Cold temperate and subalpine coniferous forest (▲), Temperate deciduous forest (●). — not included in regression (a).

Poland, field: rye (A1), potato (A2) [Golebiowska and Ryszkowski 1977], Sweden, field: barley unfertilized (A3), barley fertilized (A4), grass ley (A5), lucerne ley (A6) [Andrén et al. 1990], Georgia, U.S.A., field in winter: conventionally tilled (A7), no till (A8) [Hendrix et al. 1987].

Finland, spruce forest (C08, C09), mixed spruce forest (C02). — Sweden, pine forest (C11). — Japan, subalpine conifer forest (C48). — Sweden, grassland (G01). — Australia, pasture grazed by sheep (G65). — U.S.A., short grass prairie (G48). — Denmark, beech forest (H12). — Germany, beech forest (H19) [Ellenberg et al. 1986]. — Germany, ash-elm forest (H22). — Germany, beech forest on limestone (H63) [Schaefer 1990]. — U.K., mixed deciduous forest (H27). — Netherlands, mixed deciduous forest (H32). — U.S.A., tulip poplar forest (H59). — Canada, Devon Island, arctic tundra (T05, T06). — Alaska, U.S.A., arctic tundra, mean of several habitats (T20–T27). — U.K., montane moorland (T42, T43). — U.K., montane grassland (T44, T45). — For site descriptions and references see Petersen and Luxton [1982], appendix 1.

comprehensive ecosystem study in the tropics or subtropics has provided data on population respiration for more than a few important soil fauna groups.

If the tropical savanna site (S01) is excluded the data may be rather well described by the following allometric regression:

$$\log_{10} R = -0.81 + 0.94 \times \log_{10} B \quad r = 0.93 \quad N = 30 \quad (1)$$

where R is respiration ($\text{KJ} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$), B is dry weight biomass ($\text{mg} \cdot \text{m}^{-2}$), r is the correlation coefficient and N is number of sites.

The slope of the regression line (0.94) indicates approximate proportionality between community biomass and respiration and the regression line is very close to the line representing a weight specific respiration of 0.1 KJ per mg dwt. All but 4 sites have weight specific respiration rates between 0.06 and 0.25 kJ per mg dwt.

The close fit to the regression line is less obvious than it may seem on the background of the methodological discussion above considering the range of mean annual temperatures from -18°C at Point Barrow, Alaska, (site T20-T27) to $+13^{\circ}\text{C}$ at Oak Ridge, Tennessee, (site H59) and the differences in composition of fauna groups. Thus, the soil faunal biomass in some communities is strongly dominated by earthworms with a low weight specific metabolic rate. In other communities where earthworms are scarce or absent the fauna may be dominated by microarthropods and enchytraeids which have higher weight specific metabolic rates.

The correlation coefficients of corresponding double logarithmic regressions for individual soil fauna groups such as nematodes, earthworms, enchytraeids, springtails, Diptera larvae and mites based on data from the same sites are lower than the correlation coefficient of the total soil fauna regression. The regression equations are (cf. equation 1):

$$\text{Nematoda:} \quad \log_{10} R = -0.74 + 1.11 \times \log_{10} B \quad r = 0.71 \quad N = 18 \quad (2)$$

$$\text{Lumbricidae:} \quad \log_{10} R = -0.49 + 0.79 \times \log_{10} B \quad r = 0.88 \quad N = 18 \quad (3)$$

$$\text{Enchytraeidae:} \quad \log_{10} B = -0.81 + 0.98 \times \log_{10} B \quad r = 0.88 \quad N = 23 \quad (4)$$

$$\text{Collembola:} \quad \log_{10} B = -0.74 + 0.95 \times \log_{10} B \quad r = 0.66 \quad N = 27 \quad (5)$$

$$\text{Diptera larvae:} \quad \log_{10} B = -1.11 + 1.04 \times \log_{10} B \quad r = 0.91 \quad N = 15 \quad (6)$$

$$\text{Acarina:} \quad \log_{10} B = -1.34 + 1.07 \times \log_{10} B \quad r = 0.89 \quad N = 21 \quad (7)$$

Community respiration of the soil fauna in non-cultivated ecosystems was lowest in the arctic tundra sites and tended to increase through alpine and boreal coniferous forests to temperate deciduous forests and grasslands. This sequence can be compared with the conclusions arrived at by Kitazawa [1971] in his extensive study of regionality in community structure and metabolism of soil fauna in forest ecosystems. His work examined the biomass and community respiration of the total soil fauna in 6 different ecosystem types, placed along a latitudinal gradient in the sequence: alpine coniferous shrub, subalpine coniferous forest,

temperate deciduous forest, subtropical rain forest, tropical highland forest, tropical rain forest. While the total soil faunal biomass was relatively large in alpine and temperate shrubs and forests the community respiration was low compared with that in subtropical and tropical forests. The maximum community respiration was attained in subtropical forests. In the tropical forests, the community respiration was again lower because of very low biomass.

The highest community respiration among the data sets presented in Figure 1 originates from a Tennessee tulip poplar stand [Reichle 1977], which is classified as a warm temperate, deciduous forest. The annual mean temperature of this site is similar to the mean annual temperature of Kitazawa's subtropical evergreen forest mentioned above (15°C) and much higher than the mean annual temperatures of other temperate ecosystems considered in the present review.

The winter condition of the no-till treatment of a field in Georgia was also characterized by a very elevated soil faunal respiration [Hendrix et al. 1987]. The total soil faunal respiration of other agricultural soils, including the conventionally tilled treatment of the Georgia field, was generally lower than in the temperate woodlands and permanent grasslands.

In Figure 2 the community respiration of the total soil fauna has been related to net primary production (NPP). It is obvious that the very low plant pro-

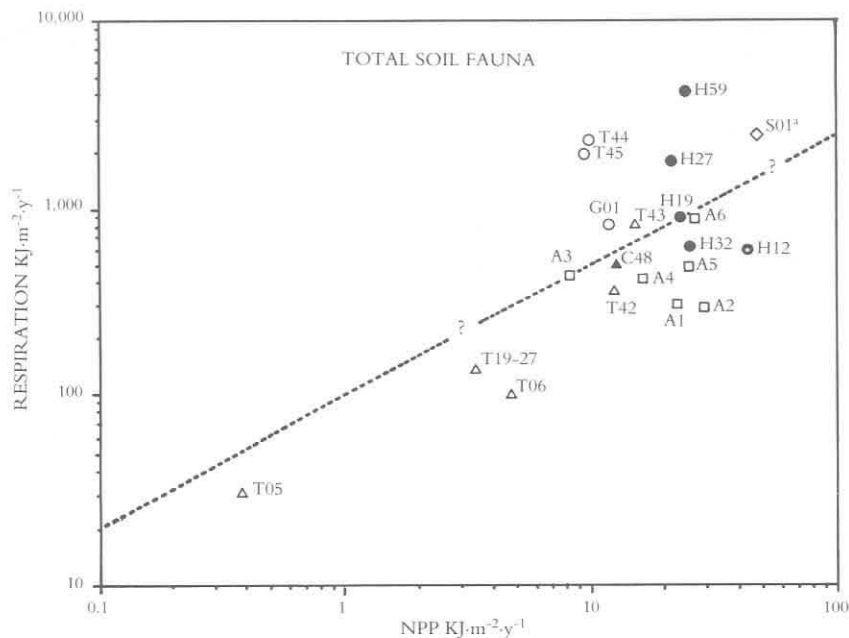


Figure 2. Relationship between community respiration of total soil fauna (excl. Protozoa) and net primary production (NPP). For explanation see Figure 1.

ductivity of arctic sites corresponds to a low soil faunal metabolism but for the majority of data available which originate from a range of different ecosystems in the temperate zone, there seems to be no clear correlation between total soil faunal respiration and net primary production.

The lack of positive correlation between the total soil faunal respiration and net primary production is also apparent from studies which include several sites or treatments examined by the same methods. Thus, at Moor House in the English Pennines, Coulson and Whittaker [1978] found that the total herbivores and decomposers had a lower annual respiration in two sites on peat soil, than in two grassland sites on mineral soil, whereas the primary production was highest in the two sites on peat soil.

Golebiowska and Ryszkowski [1977] found a higher soil faunal respiration in a rye field than in a potato field which had higher net primary production. In the experimental field of the Swedish agro-ecosystem study [Andrén et al. 1990] the NPP of the fertilized barley plots was twice that of the unfertilized barley plots, whereas the total soil faunal respiration of the former was slightly less than that of the latter. In the lucerne ley plots, however, both NPP and total soil faunal metabolism were higher than in the rye and the grass ley plots.

The community respiration of the total fauna was not significantly corre-

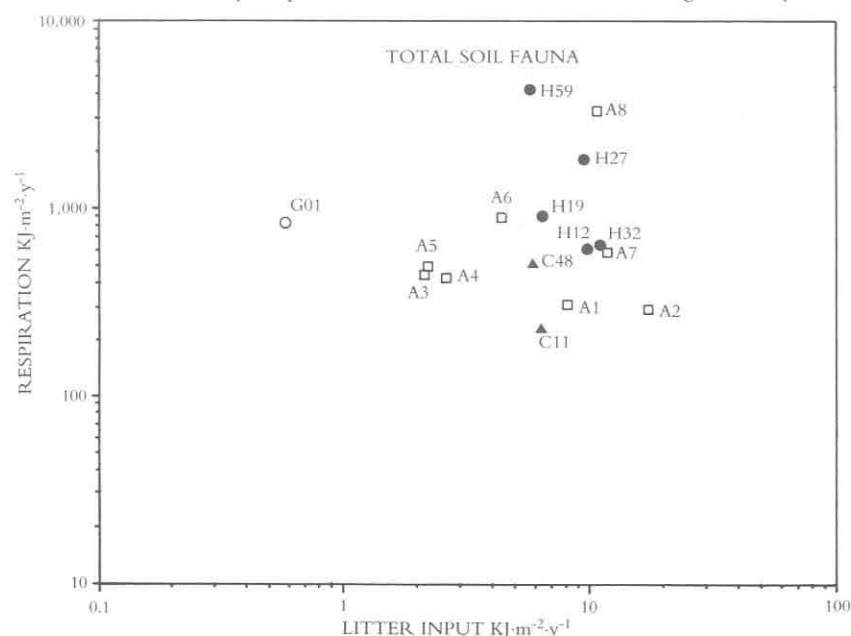


Figure 3. Community respiration of the total soil fauna (excl. Protozoa) plotted against litter input to the soil surface. For explanation see Figure 1.

lated with litter input to the soil surface [Figure 3]. There were insufficient data available for an examination of possible correlations between the amounts of accumulated soil organic matter and total soil faunal respiration but in a comparison of forest ecosystems Petersen and Luxton [1982] showed a negative correlation between accumulated organic matter on the soil surface and soil faunal biomass.

Energy Flow Through the Decomposer Food Web

It is a fundamental objective for ecosystem studies to integrate the results obtained in many specialized studies into a coherent description of the ecosystem as a whole. Energy flow is the basic biological process which links all organisms in the ecosystem together and is a condition for all other biological processes. It is therefore of greatest interest to understand how the energy fixed by the photosynthesis of green plants is transferred through the ecosystem.

The great obstacle for the study of energy flow is the enormous complexity which characterizes nearly all ecosystems. The decomposer food web, which is based on the dead organic matter input from plants, microorganisms and animals, is at least as complicated as the herbivore food web based on living green plants. For instance, about 75 species of nematodes [Yeates 1972], 175 species of mites [Luxton 1982] and about 60 species of Collembola [Petersen 1980] were recorded in an extensive soil sampling programme within the 3 hectares of the Danish IBP beech wood research site, as well as a great number of soil faunal species belonging to other taxa. About 500 animal species or groups were identified in the German beech forest site at Solling (both below and above ground), but the total number of species was estimated at 1,500 to 1,800 [Ellenberg et al. 1986]. Even if the rare occurrences are sorted out, the web of food relationships at the species level is boundlessly complicated.

The need for simplification has usually been overcome by using larger taxonomic or functional groups of species as units for the energy flow analysis or by classifying the organisms into trophic levels in spite of the weakness of this concept [Rigler 1975].

Computer modelling is a potentially useful tool for comprehending processes in a complex system [O'Neill 1979] and has the most valuable quality, that it helps the research worker to consider thoroughly the parameters needed in order to understand the function of the system [Berthet 1977]. Ecosystem models, even those focusing on decomposition [e.g. Hunt 1977], have generally not included the soil faunal groups specifically as state variables of the system and Andrén et al. [1990] conclude that it is possible in their agro-ecosystem to model decomposition as well as mineralization and immobilization of nitrogen accurately, without considering the organisms in the system, because the effect of the

organisms is contained in the controlling factors (temperature, moisture, resource availability) used in the model.

With R.V. O'Neill and R.H. Gardner (Oak Ridge National Laboratory, U.S.A.) the author developed a linear biomass model [Petersen et al. 1985] based on data from an extensive, multidisciplinary ecosystem study of a typical Danish beech forest carried out as a contribution to the International Biological Programme. The model puts some emphasis on the energy flow through the soil fauna community which was studied in fairly great detail by the joint effort of a team of research workers [Petersen and Luxton 1982].

The result was a model composed of seventy differential equations, one for each component of the system, defined by compromising between simplicity and conservation of some of the complexity characteristic of the ecosystem [Petersen et al. 1985]. Thus, although the soil fauna was treated basically as larger taxonomic groups (nematodes, collembolans, oribatid mites etc.) several of these were split into trophic subgroups, based on results from laboratory-feeding experiments or gut analyses [e.g. Luxton 1972]. The dead organic matter was divided into five fractions with different turn-over times: leaf and seed litter, branch and bole litter, root litter, detritus and humus. The turn-over times were estimated as 1.7, 5.2, 1.7, 1.0 and 500 years, respectively [Petersen unpublished].

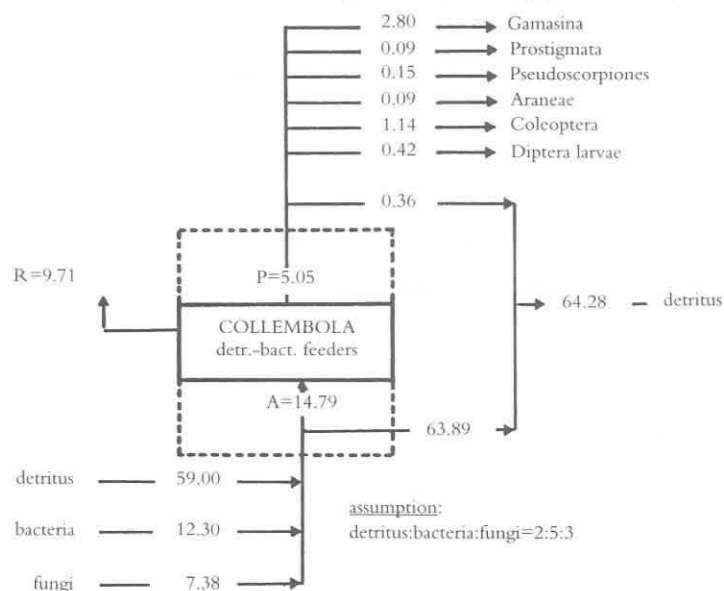


Figure 4. Energy flows ($\text{KJ} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) through one taxonomic-trophic compartment of the Hestehave beech forest model (detritus-bacterial feeding Collembola). Assimilation (A), Production (P), Respiration (R).

Figure 4 shows the energy flow through one example of a soil fauna compartment in the ecosystem model. Based on the author's own observations of collembolan gut contents [Petersen unpublished] the Collembola has been divided into three trophic groups: fungal feeders, detritus-bacterial feeders and litter-microphytophages. The majority of euedaphic and hemiedaphic Collembola have been classified as detritus-bacterial feeders. Respiration (R) was calculated from field data of biomass and size structure of each species classified in this trophic group by means of species specific regressions relating oxygen consumption to weight and temperature [Petersen 1981]. Production (P) and assimilation (A) was calculated from R according to the P/R-ratio for non-insect detritivores in Humphreys [1979]. The proportions assimilated from the intake of detritus, bacteria and fungi, respectively, has tentatively been assumed to be 2 : 5 : 3. The consumption (C) and defecation (F) rates were then calculated assuming that assimilation efficiencies (A/C) for the three kinds of food were 0.05, 0.6 and 0.6, respectively. For predators, the calculation was similar in principle. Different kinds of prey were assumed to be consumed by a predator in proportion to their production rate. In this way the predation on detritus-bacterial feeding Collembola was found from the consumption rates of likely predators.

The behaviour of the biomass model was examined by comparing the initial state with the final state after a simulation period of 300 years [Petersen et al. 1985]. In that paper it was demonstrated how the model can be used to validate the estimate of fine root production and to examine the effect of changing the

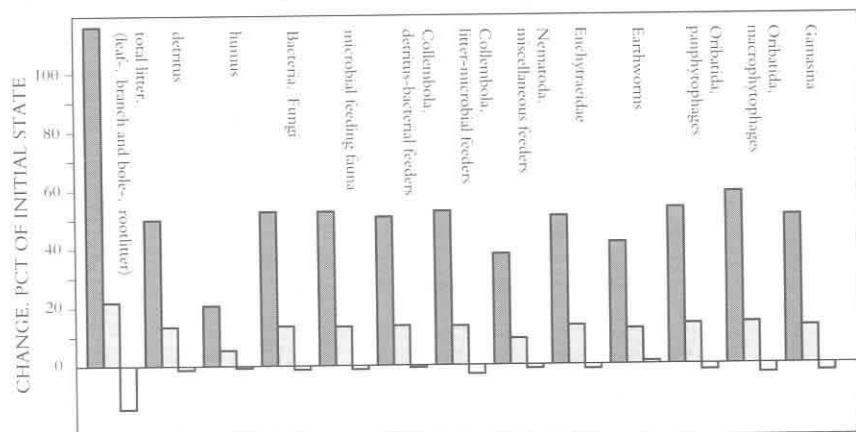


Figure 5. Response of the Hestehave beech forest model if continued harvesting of boles is assumed. The columns show the calculated change as percent of the initial state value after a simulation period of 300 years. — Primary, i.e. unmodified model (black columns), — Boles harvested, branches remain on forest floor (hatched columns), — Boles harvested, branches removed (open columns).

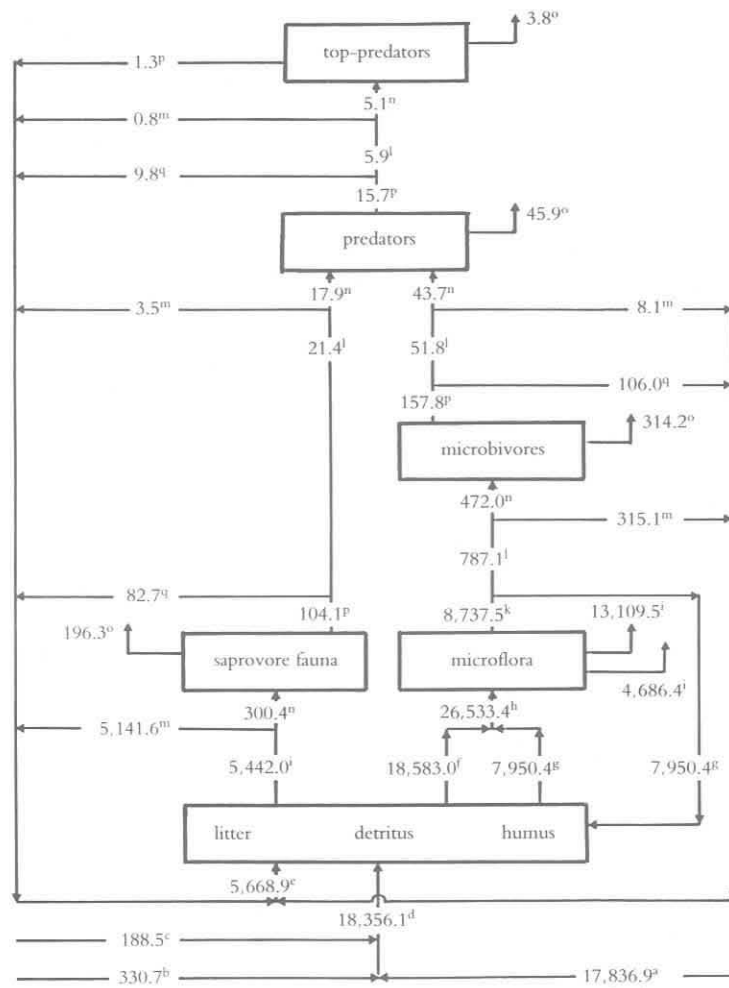


Figure 6. Hestehave beech wood: Energy flow through soil biota ($\text{KJ} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$), — a. total litter input (incl. leaf-, wood- and root litter), — b. input from above-ground fauna, — c. input from below-ground herbivores and their predators, — d. total input to soil, — e. total faunal recirculation, — f. primary microbial utilization, — g. microbial recirculation, — h. total microbial utilization, — i. microbial maintenance, — j. microflora, respiratory cost of production, — k. microflora, total production, — l. faunal consumption, — m. faunal defaecation, — n. faunal assimilation, — o. faunal respiration, — p. faunal production, — q. fauna, non-predatory mortality (recirculation).

biomass, production and respiration of the microflora.

The unmodified model leads to considerable accumulation of dead branches and boles but the detritus only increases half as much as the combined litter

compartments and the humus again increases half as much as the detritus [Figure 5, black columns]. A similar damping effect was not observed through the trophic levels, from detritus through microflora and microbivores to predators. All these compartments increased by about 50%, with slight differences related to variations in the composition of various food components. Thus, earthworm biomass increased relatively little, because dead wood had not been included as part of their diet. The opposite was true for macrophytophagous oribatids as result of a high proportion of branch and bole litter in their food.

Figure 5 (hatched and open columns) shows the predictions of the model if boles are harvested at the same rate as usual in Danish forestry. If branches are left on the forest floor a small increase is seen in all compartments. If the branches are removed litter, detritus, humus and all organisms in the decomposer food web decrease slightly.

A submodel for the energy flow through the decomposer food web where all components at the same trophic level have been summed to composite trophic levels is shown in Figure 6. The microflora part was used for calculating microbial production, based on the model proposed by Heal and MacLean [1975] according to Kj  ller and Struwe [1982]. The fundamental assumption is that the system is in a steady state, i.e. that all energy input to the soil organic matter pool (litter/detritus/humus) is dissipated by respiration. The part of the production which is not consumed at the next level (non-predatory mortality) is recirculated back to the soil organic matter pool together with the part of the consumption which is not assimilated, i.e. the faeces. The recycled energy will then be assimilated by the microflora and used for new production and respiration. The cycling will continue until all energy has been dissipated as respiration.

Calculations on a personal computer can simulate the cycles until a selected minimum value for e.g. microbial production is reached. Thus, by using the original data from the Danish beech wood site the model will pass through 11 cycles before a minimum microbial production value of $0.1 \text{ KJ} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ is reached [Table 1]. The saprovores fauna was omitted in these simulations.

It is possible to examine the effect of changing one or more of the parameters in the model. Table 1 shows that increasing the predation pressure (predation/production) on the microflora (identical to consumption efficiency of microbivores) from 0.09 to 0.9 will lead to a reduction in the number of cycles, a slight reduction of microbial production and 8-9 times higher production of microbivores, predators and top-predators. Total production of the decomposer organisms will remain unchanged. The result may be understood as an acceleration of the decomposition process. Increase of the predation efficiency to 0.9, for all trophic levels, gives nearly the same result for the microflora and the microbivores as seen in the previous experiment, but very strong increments of production in predators and top-predators.

Table 1. Effects of energetic efficiency ratios on recycling and productivity in the soil community. Arrows indicate changes from the original efficiency ratio. (pred/P=ratio of predation by higher trophic levels to production, A/C=assimilation efficiency, R/A=proportion of assimilation respired)

energetic efficiency ratio (trophic level)	change from original efficiency	no. cycles	change of production (P) [times more (×) or less (÷) than original data]				
			micro-flora	microbi-vores	predators	top predators	all organisms
original data	~	11	1	1	1	1	1
pred/P (microflora)	0.09→0.90	8	÷ 1.18	× 8.5	× 8.5	× 9.1	÷ 1.004
pred/P (all levels)	(0.09-0.38)→0.90	8	÷ 1.22	× 8.2	× 22.4	× 56.9	÷ 1.01
A/C (microbivores)	0.60→0.10	11	× 1.02	÷ 5.9	÷ 6.3	÷ 4.8	× 1.0005
R/A (microflora)	0.67→0.50	17	× 2.0	× 2.0	× 2.0	× 2.1	× 2.0
R/A (all fauna)	(0.60-0.75)→0.50	11	× 1.004	× 1.5	× 2.0	× 4.3	× 1.02

Reduction of the assimilation efficiency of microbivores, for instance from 0.6 to 0.1, has little effect on the microflora but, naturally, the productivity of the higher trophic levels becomes reduced. If the decrease in assimilation efficiency, however, is compensated by a corresponding increase in consumption efficiency, no changes are observed for any trophic level. That is because the model does not distinguish between energy recirculated through non predatory mortality or through defecation of the microbivores.

Alteration of the respiration/assimilation ratio for all faunal groups has an insignificant effect on microbial production but has increasing effect through the trophic hierarchy from microbivores to top predators. A decrease of this ratio for the microflora from 0.67 to 0.5 results in a doubling of production at all trophic levels, and an increase in number of cycles from 11 to 17. This may be interpreted as a deceleration of the decomposition process.

This kind of exercise, as well as ecosystem modelling as a whole, is useful for identifying the possible mechanisms, relationships between different phenomena, probable limits for parameter values etc. and for bringing up questions which may lead to profitable hypotheses to be tested in the laboratory or in the field. The model may also produce secondary integrated quantities which characterize a complex of processes. Thus, in the present model the number of cycles makes up an index of decomposition rate which may characterize different ecosystem types and stages of ecosystem succession. It may also be useful as an indicator of ecosystem disturbance or stress, caused for instance by pollution. For these purposes, however, much more experimental data are needed about the variability of the metabolic efficiencies among species and how the efficiencies are controlled by environmental factors.

The assumption of the present rather primitive model, that microbivore consumption followed by defecation has the same effect on the total energy flow as non predatory recirculation from the microflora, is questionable. The model

does not consider the way the energy is bound in the organic matter or the availability of other resources such as nutrients necessary for the utilization of the energy. Thus, the quality of the soil organic matter as a substrate for utilization by the microflora does not influence the outcome of the model.

The model does not account for the fact either that most microbivores have to consume a great quantity of the substrate in which the bacteria and fungi live, in order to extract the required nutrition, and that the passage of this mixed dead and living material through the gut of the animal does not generally lead to net mortality of the microflora. More often, the passage through the gut results in stimulation of microbial productivity, as consequence of, for instance, comminution and increased $\text{NH}_4\text{-N}$ and carbohydrate levels. This stimulation of microbial activity in the gut and faeces, which is generally accompanied by qualitative changes in the composition of the microflora has been thoroughly reviewed by Visser [1985].

Evidence of such indirect effects of the decomposer fauna, which greatly overshade the generally modest direct contribution of the fauna to soil community respiration, has accumulated during the last decade [e.g. Hanlon and Anderson 1979, Anderson and Ineson 1983, Seastedt 1984, Ingham et al. 1985] but this kind of information seems still to be at too general a level to be applied quantitatively in models of energy flow. Some doubt has also been expressed as to the role of the decomposer fauna in controlling decomposition and mineralization in the complex field situation. Thus, Andr  n et al. [1990] had to leave the question open as to whether most species of soil organisms are "unnecessary" from a system's viewpoint so that decomposition and mineralization will proceed at the same rate regardless of whether they are involved or not. Persson [1989] added a mixed soil arthropod fauna to microcosms, with material of the F/H horizon from a Norway spruce stand from which soil arthropods had been removed. No increase of CO_2 production was observed, whereas the presence of soil arthropods increased the mobilisation of inorganic N at all temperatures and moisture conditions significantly.

General Discussion and Conclusions

Prospects for Future Energy Flow Studies

The review and above discussions may leave the impression that the energy flow of the total soil fauna community, expressed as community respiration, is relatively well known for natural and semi-natural ecosystems in arctic and temperate climate zones. The community respiration of agricultural fields fits well into the distribution of respiration data from natural ecosystems but is generally lower than that found in natural ecosystems of the same climatic zone. There is still a lack of information about the total soil faunal respiration in both

natural and managed subtropical and tropical ecosystems, but one study [Kitazawa 1971] suggests that the highest total soil faunal respiration may be expected in humid subtropical evergreen forests.

Correlations between total soil faunal respiration and net primary production are weak or non-existent except when comparisons are made between extremely unproductive ecosystems such as arctic tundra and more fertile ecosystems in, for instance, the temperate climatic zone. Similarly, there appears to be no clear correlation between litter input to the soil surface and total soil faunal metabolism, whereas in forest soils the total faunal biomass and probably also the total faunal respiration is correlated negatively with top soil organic matter. This phenomenon may be explained by the impoverishment of the earthworm fauna in mor and moder soils [Petersen and Luxton 1982].

Energy flow studies in strongly disturbed environments and their succeeding stages of recovery, may give insights into the way that food webs and energy flow patterns in the soil develop. Great interest has been shown lately in the succession of community structure in such situations, but, except for the study of Dunger [1968], no comprehensive study of soil faunal metabolism in such situations has been carried out.

Perhaps the most crucial problems for ecosystem studies is the lack of independent, field-related estimates of the parameters in the energy flow equation. The majority of estimates available at present may be considered as merely field biomass and density data, transformed into quantities of energy flow by means of largely the same set of efficiency ratios obtained in laboratory experiments. For soil animals, only a few examples exist of secondary production estimates based on the analysis of growth and mortality of even-aged cohorts of the field population. One of these [van Straalen 1989], suggests that the traditional methods based on laboratory estimates of efficiency ratios may sometimes have underestimated the metabolic rate of field populations.

One of the most urgent tasks is to estimate consumption rates in the field in connection with identification of the qualitative composition of the food and the assimilation efficiency of each kind of food item. Lavelle [1975] was able to estimate the consumption rate of the geophagous West African earthworm *Millsonia anomala* from measurements of faecal pellet production in sieved soils. In this way, he found very high ingestion rates of up to 30 times the body weight per day, depending on temperature, humidity and developmental stage. On the other hand, assimilation efficiency was very low (0.09 according to Lamotte 1989). It is not unlikely, that corresponding field methods would show that other geophagous, humivorous or saprovorous soil animals utilize their natural food, i.e. soil organic matter, with its contained microflora, with similar low efficiencies. Low assimilation efficiency means that the amount of material ingested has to be high in order to supply the population with enough energy for metabolism

and production. Therefore, the effect of a population on its food substrate will be correlated negatively with its assimilation efficiency.

Quantification of the indirect controlling effects of the soil fauna on the microflora is another challenge for future studies of energy flow through the soil community. Experiments based on manipulations of the soil community, such as by exclusion of selected populations from the field community, or combination of selected populations in field or laboratory microcosms, are promising options for this purpose.

Better methods for estimation of microbial biomass and metabolism would be highly desirable in understanding energy flow through the whole soil community but, on the other hand, it is not unlikely that more exact information about feeding rates of microbivores may also assist in the estimation of microbial production by setting minimum values needed to feed the microbivore population. Thus, soil microbiology and soil zoology may contribute mutually to the quantification of productivity in the soil community, which consequently should lead to a better understanding of the energy and nutrient dynamics in the ecosystem.

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